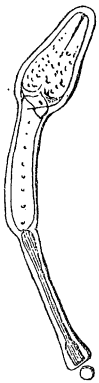
THE HOMOLOGIES OF PEDICELLARIÆ.

BY ALEXANDER AGASSIZ.

O. F. Müller, in his "Zoologia Danica" was the first to point out the existence of certain organs in sea-urchins which have long remained a puzzle to naturalists. To these organs he gave the generic name Pedicellaria, and considered them as parasites of the sea-urchins. Of his genus Pedicellaria he describes three species which are now known to be either different stages of development, or different kinds of pedicellariæ, situated in various parts of the shell of the sea-urchin. Our knowledge of the pedicellariæ is now materially changed, first by the views of Delle Chiaje, who, in 1825, figured and described the pedicellariæ of several sea-urchins and starfishes. He however no longer considers them simple parasites but says distinctly that they form a part of the test of the Echinoderms and help them in seizing their prey and taking hold of adjoining bodies. Much of this view has been corroborated, and like many of the shrewd observations of Delle Chiaje is gaining only now the recognition it should have received long ago. Valentin in 1841 gives in his "Anatomy of Echinus" excellent figures and descriptions of pedicellariæ which he considers as organs of prehension. Agassiz at that time suggested the possibility of their being young stages of Echinoderms, in consequence of the discoveries then made by Sars of the remarkable development of a species of starfish. This, it is needless to say, is a view he has long ago abandoned though he is most persistently credited with it even at the present time. Subsequently, Erdl, Duvernoy, Müller and Troschel, Sars, Stimpson, Norman and Stewart have figured a number of pedicellariæ of Echini and starfishes, and have made a more or less successful attempt to use their characters as aids in distinguishing closely allied species. An article on pedicellariæ in the "Annales des Sciences Naturelles" for 1869, by Perrier, gives a large number of excellent figures of the pedicellariæ of starfishes and sea-urchins; unfortunately, except as a mere accumulation of facts, it is useless, the writer ignoring what had been done for the last twenty years, on the very appendages he was describing, so that he leaves the question of their nature

as it stood in the days of Valentin in spite of the many observations made, and hints of their true nature thrown out by Müller, Troschel, Sars and A. Agassiz, which would have saved Perrier much useless speculation.

Fig. 78.



No attempt has yet been made to ascertain the homologies of these organs, and the present article is intended to give the results which have been reached by the writer since 1864, from the study of the embryology of starfishes and Echini.

Fig. 79.

If we examine the common sea-urchin of the coast of New England, we shall find, scattered in between the spines over the whole surface of the shell, numerous pedicellariæ (Figs. 78 and 79). They consist of a calcareous stem (Fig. 80) articulating at its base upon a small granule of the test; this is surrounded by a muscular sheath expanding into a somewhat swollen portion with a thimble-shaped knob at the end. This knob, though it seems solid and compact at first sight, is in reality split into three wedges (Fig. 81 *a*), which can be opened and shut at will. When open, these pedicellariæ may be compared to a three-pronged fork, except that the prongs are arranged concentrically instead of on one plane and when closed they fit into one another as neatly as the pieces of a puzzle. Fig. 81 represents the end view of one of these pedicellariæ.

Fig. 81 *a*.

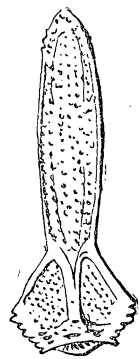


Fig. 80.

If we watch a sea-urchin after he has been feeding, we shall learn at least one of the offices which this singular organ performs in the general economy of the animal. That part of the food which he ejects passes out of the anus, an opening on the summit of the body in the small area where the zones of which the shell is composed converge. The rejected particles, thrown out in the shape of pellets, are received on these little forks which close upon them like forceps, and they are passed from one to the other down the side of the body till they are dropped off into the water. Nothing is more curious and entertaining than to watch the neatness and accuracy with which this process is performed.

Fig. 81.

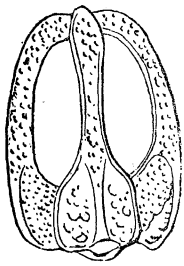
One may see the rejected bits of food passing rapidly along the lines upon which these pedicellariæ occur in greatest number, as if they were so many little roads for the conveying away of the refuse matter; nor do the forks cease from their labor till the surface of the animal is completely clean and free from any foreign substance. Were it not for the pedicellariæ the food thus rejected would become entangled among the tentacles and spines, and remain stranded there till the motion of the the water washed it away. These curious little organs have other offices besides this very laudable and useful one of scavenger. They occur over the whole body, while they pass the excrements only along certain given lines. They are especially numerous about the mouth where they are much shorter (Fig. 79) and more compact; the muscular sheath below the head is quite short, the tripartite head resting directly upon the limestone rod of the base.

Fig. 82.

Fig. 83.

On watching the movements of the pedicellariæ we find that they are extremely active, opening and shutting their forks unceasingly, reaching forward in every possible direction, the flexibility of the sheath enabling them to sweep in all the corners and recesses between the spines, and occasionally they are rewarded by catching hold of some unfortunate little crustacean, worm or mollusk which has become entangled among the spines. They do not seem to pass their prey to the mouth (at least I have never succeeded in seeing sea-urchins pass the food thus caught), but merely throw it off from the surface like any other refuse matter. Their mode of eating, also, a sort of browsing, by means of their sharp teeth along the surface of the rocks, does not favor the idea of using the pedicellariæ as forks.

Fig. 84.



Among the different kinds of sea-urchins we find a great many modifications of the pedicellariæ just described. In the genus Cidaris the muscular sheath below the head is short and slender (Fig. 82); it is placed upon the summit of a limestone rod made up of bundles of longitudinal rods. In some Spatangoids the

separate prongs are toothed and ornamented (Fig. 83, *Brissus*). We frequently find, both in the common spherical Echini and in the Spatangoids, the forks forming either open arches, as in Fig. 84, *Echinocardium*, or very complicated ball and socket joints, or independent hemispheres with sharp grooved edges (Fig. 85, *Pourtalesia*). In our flat cake urchin (*Echnarachnius*) the more common pedicellariæ have but two forks, with sharp teeth along the edges (Fig. 86).

Fig. 85.

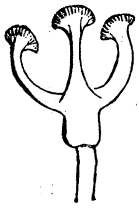


Fig. 86.

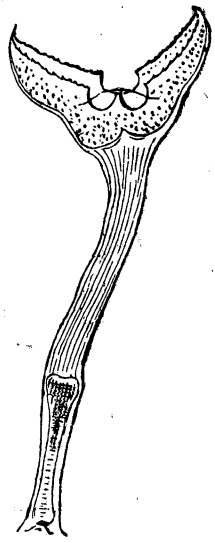
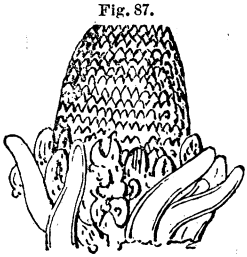


Fig. 87.



In the greater number of starfishes the pedicellariæ are supported upon comparatively short stems, and are as in our common starfish (*Asteracanthion*) clustered round the base of the spines of the dorsal surface (Fig. 87); though in starfishes we also find tripartite pedicellariæ as in sea-urchins, only they are usually supported upon a very short stem, or articulate directly from the limestone network of the shell. We find similarly in Echini pedicellariæ placed in pits (*Goniocidaris*) in which the stem is reduced to a minimum, and their function is quite problematical; their movements are reduced to the mere opening and shutting of the valves. It is from the study of the pedicellariæ of starfishes that we have been able to form some accurate idea of the homologies of these interesting appendages.

Fig. 88.

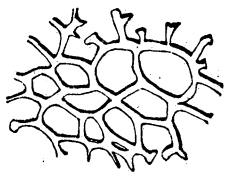
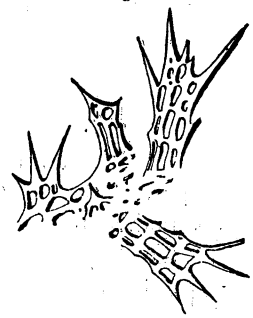


Fig. 89.



We must now go back to the early history of the growth of spines in embryo Echinoderms to obtain the key of the homologies of pedicellariæ. In all young echinoderms the test, *i.e.* the

upper coating of the arms of a starfish, the envelope of a Holothurian, the shell of a sea-urchin, is made up of an irregular network of limestone cells (Fig. 88); with increasing size this network becomes closed at certain points and sends off upright shanks which little by little form very irregular fan-shaped spines (Figs. 89 and 90); in our common sea-urchins these spines are immovable, forming at that stage part of the test itself. As the spines grow they become more pointed (Fig. 91) but are still immovable. In somewhat more advanced stages a slight constriction is formed at the base of the spine (Fig. 92) and very soon after that, below the constriction a tubercle is formed upon which the spine is articulated and capable of a certain amount of motion by means of the muscular sheath connecting the base of the spine and the tubercle, which fit by a ball and socket joint (Fig. 93); soon the spine appears longitudinally striated, the limestone cells of which it was composed when smaller being obliterated by the successive circular layers of the older spine (Fig. 94).

Fig. 90.

Fig. 91.

Fig. 92.

Fig. 94.

In some sea-urchins (*Arbacia*) we find spines which never become articulated, are always fixed, and remind us of the embryonic stage of the spines of our common sea-urchin. In one of the Echini discovered by M. Pourtalès the fixed spines cover the whole upper part of the test (Fig. 95), the movable spines being limited to a circumscribed area along the edge of the shell (Podocidaris).

Fig. 93.

Fig. 95.

If we trace the development of the spines of starfishes, we find something similar; but as the pedicellariæ are clustered round the base of the longer spines, we are able to distinguish in the earliest stages what will become a spine, and what will eventually form pedicellariæ, a distinction which it is not possible to make in Echini where the pedicellariæ and spines are irregularly

scattered. This is especially the case in such genera as Arbacia and the like, in which there are so-called embryonal spines remaining always fixed immovably to the test.

Fig. 96.

Fig. 97.

In our common starfish I have traced the earliest stages of the spines and pedicellariæ (Fig. 96), and have found that at first it is impossible to distinguish between a spine and pedicellariæ; it is only in somewhat later stages that the first trace of a difference can be detected (Figure 97); subsequently there is no doubt whatever, owing to the greater and more rapid development of the central spine, as to what will form spines or pedicellariæ (Figure 98). In one of the pentagonal starfishes of our coast (*Hippasteria*) it is even easier to trace the gradual passage of the original limestone network either, on the one hand, into a spine, or, on the other, into bipartite pedicellariæ.

Fig. 98.

Fig. 99.

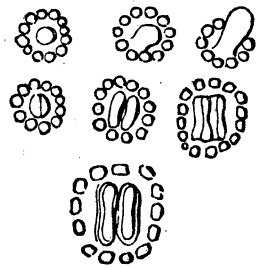
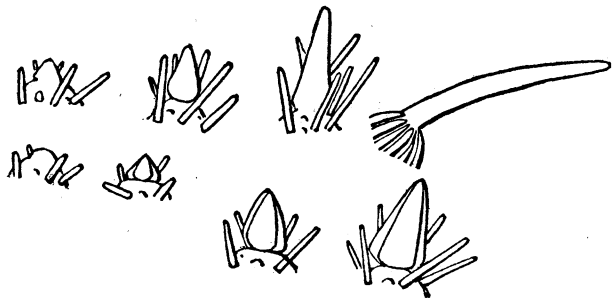


Fig. 100.

Fig. 101.



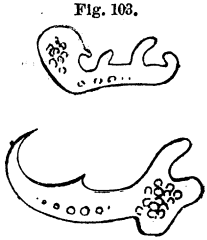
In Fig. 99 we can easily trace the development of a simple central granule, surrounded by smaller granules, into a short spine, or by the splitting of the granule we have gradually formed a slight furrow, then a deeper groove, till two clappers are formed

(Fig. 100) which eventually become movable and act as pedicellariæ, though they are the simplest forms of that organ. In another starfish, the genus Luidia, the central granule surrounded by smaller granules develops either into a spine which passes through the stages of Fig. 101, and terminates in a long slender spine surrounded by papillæ at its base, or the central spine of Fig. 101 is like the central granule of Hippasteria, little by little split into three, and forms finally a passage through such forms as are given in Fig. 101 into short tripartite pedicellariæ surrounded by isolated spines at the base. If anything further were required to prove the homology between spines and pedicellariæ it is the case of tripartite, pedunculated Echini pedicellariæ attached, as common spines are, upon a tubercle (Fig. 93) surrounded by the peculiar smooth area called the scrobicular circle; and this last form of pedicellariæ is actually found in the genus Podocidaris (Fig. 102). The same reasoning will readily suggest to the student of Echinoderms the homology of the so-called claws of Ophiurans (Fig. 103) and of the anchors of Holothurians (Fig. 104) which, although used for such totally different functions, being a sort of prehensile organ, for motion along the ground, are in reality only in their turn modified spines, or different forms of pedicellariæ.

Fig. 102.

Fig. 104.

Fig. 103.



Although the spine (Fig. 94) of our common sea-urchin is apparently so different from the pedicellariæ figured in this article, yet when we pass in review the whole order of Echini we find differences among the spines fully as great as those observed in the pedicellariæ. What can be more diverse than the immense, slender, hollow spine of a Diadema six to eight times the diameter of the test, and the short, flattened spine forming a regular pavement on the test of Colobocentrotus. We find such extremes as the club-shaped, curved, ambulacral spines of Salenia, the papillæ of Cidaris, the sharp, solid, curved, antennæ-like spines

of Coelopleurus, the massive, bat-shaped spines of Heterocentrotus, the cupuli-form spines of Goniocidaris, the slender, silk-like spines of the Clypeastroids. Among the Spatangoids, there are several families where the spines are specialized along certain lines (the so-called fascioles) in which they so retain their embryonic features, being either articulated (Fig. 105) or directly attached to the test, and provided at the extremity and along the shaft with a more or less sensitive vibratile membrane, as all young spines originally are.

In Ophiurans we find all the intermediate stages between plates, claws and slender spines; in starfishes between the simplest granules, the most complicated serrated spines and pedicellariæ, and in Holothurians, between mere spicules, anchors and the pavement-like covering of such genera as Cuvieria and Psolus. All this shows plainly enough that the spines and pedicellariæ are strictly homologous, whatever modifications they may assume in the different orders of Echinoderms, whether they serve as prehensile scavengers or simply protect the test against the violence of the waves on the rocks, or the attacks of their enemies. Sea-urchins are favorite food of many species of fish who would find it rather dangerous to attack the bristling Diademas and require pretty strong jaws to get the better of the armored Heterocentrotus. The spines are not simply organs of defence; they also act as means of locomotion, and in such genera as Arbacia the ambulacral suckers perform only a secondary part in the displacement of the sea-urchin, the spines of the lower side serving as stilts by which the sea-urchin raises itself and moves along by a kind of halting gait. In Ophiurans and Holothurians, the pedicellariæ hooks and anchors perform the part of organs of prehension and locomotion at the same time.

Fig. 105.

There is nothing in the history of the development and in the homologies of these organs to show that they have been suddenly brought into existence; on the contrary, the modifications of the spines and pedicellariæ as they have been rapidly sketched in this article show the most complete homology between appendages which have lately been considered as strong proofs of the possibility of the sudden appearance of organs for which no utilitarian motive could be given. I trust I have made it sufficiently plain

that in the most complicated pedicellariæ known, with a freely movable stalk and with snapping jaws, we have only a very gradual modification of the simplest sort of limestone network found in all Echinoderms in the earliest stages of the embryonic development, while still in the Pluteus-stage, and that we have an unbroken sequence from this primitive network to form, on the one side the most diversified spines, and on the other equally variable pedicellariæ, and that we must consider the latter in their most complicated forms as nothing but highly specialized spines.

REVIEWS AND BOOK NOTICES.

THE DEPTHS OF THE SEA.* — One could not but form a favorable impression of this sumptuously printed book from its attractive exterior; the pleasant impression is deepened by a perusal of it. The narrative is on the whole clear and graceful: the novelty of the facts and the fine illustrations will interest the lay reader, and the scientist will find placed before him in an accessible form the results obtained by the British explorations by means of the dredge and thermometer in the depths of the eastern north Atlantic and the Mediterranean Sea.

The marine zoologist will be led after reading it, as perhaps not before, to study more carefully the temperature and chemistry of the water in which he dredges, while the broader questions of the geological and geographical distribution of animals will engage his attention perhaps the more after reading Prof. Thompson's interesting summary of the joint work done by Carpenter, the physiologist and physicist; Jeffreys, the conchologist; and Wyville Thompson, the accomplished zoologist. After the introduction, we have chapters giving an account of the cruise of the "Lightning," those of the "Porcupine;" chapters on deep-sea sounding, and deep-sea dredging, on deep-sea temperatures, the Gulf Stream, the deep-sea fauna, and the continuity of the chalk.

In the introduction (p. 44) the idea is presented that deep-sea

*The Depths of the Sea. An Account of the general results of the Dredging Cruises of H. M. S.S. "Porcupine" and "Lightning" during the summers of 1868, 1869, and 1870, under the scientific direction of Dr. Carpenter, J. Gwyn Jeffreys and Dr. Wyville Thompson. By C. Wyville Thompson. With numerous illustrations and maps. New York and London, Macmillan & Co., 1873. 8vo. pp. 527. (The illustrations are in part here reproduced, thanks to Messrs. Macmillan, the publishers.)